



Annual and seasonal dynamics of deep-sea megafaunal epibenthic communities in Barkley Canyon (British Columbia, Canada): A response to climatology, surface productivity and benthic boundary layer variation

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ABSTRACT

Understanding the impact of the environment on temporal trends in the composition and abundance of deep-sea species is essential for forecasting evolution of the community in the context of climate change. The recent development of deep-sea observatories enables multidisciplinary studies of long duration and high temporal resolution. We used a platform at the Ocean Networks Canada NEPTUNE Observatory located in the axis of Barkley Canyon between June 2012 and January 2015 to: (1) characterize the megabenthic community and the environmental conditions in the canyon; (2) investigate temporal patterns in the faunal community; and (3) determine the influence of environmental conditions on the observed patterns. The megafaunal epibenthic community, which included commercially important species, was composed of species known to be able to adapt to low oxygen conditions. A strong seasonal pattern characterized wind speed and direction, wave height, temperature, and chlorophyll concentration at the sea surface. The megafaunal epibenthic community exhibited seasonal patterns which were influenced by in-situ benthic boundary layer currents and temperature, weather conditions and chlorophyll concentration at the sea surface. At inter-annual scales, the surface temperature anomaly event observed in 2013 in the region could potentially impact the community structure with significant changes in species' densities, highlighting the need for long-term monitoring in the region.

1. Introduction

Submarine canyons are elongated, narrow, steep-sided depressions that generally deepen down-slope (IHO, 2013). They incise the continental shelf and slope along all continental margins covering a total area of 4,393,640 km², which represents 1.21% of the ocean floor and 11.2% of continental slopes (Harris et al., 2014). The importance of canyons as providers of ecosystem services was recently reviewed by Fernandez-Arcaya et al. (2017). The complexity of the topography and the heterogeneity of the substrate, in addition to food input, promote a higher abundance, biomass and diversity of organisms in most canyons compared to the adjacent slope (De Leo et al., 2014, 2012; Paine et al., 2014; Puig et al., 2015). Canyons can also provide shelter (Farrugio, 2012), and areas for recruitment (Fernandez-Arcaya et al., 2017, 2013; Puig et al., 2001) and feeding (Ross et al., 2015) for some fish and crustaceans. Unfortunately, these services are threatened by human activities, such as fishing, oil and gas exploitation, and pollution (Fernandez-Arcaya et al., 2017; Martín et al., 2014; Paine et al., 2014; Ramirez-Llodra et al., 2011; Van den Beld et al., 2016). Climate change,

by increasing the number and intensity of extreme events, is also predicted to affect canyon communities (Cheung et al., 2010; Danovaro et al., 2001; Ruhl and Smith, 2004). A better understanding of the diversity and dynamics of canyons is thus critical for predicting anthropogenic impact on the ecosystem structure and dynamics.

While most studies in canyons have investigated the role of hydrodynamics, habitat complexity and food availability on the spatial distribution and structure of benthic communities (Duineveld et al., 2001; Gage et al., 1995; Vetter and Dayton, 1999), only a few have focused on temporal dynamics (Aller and Stupakoff, 1996; Blanchard et al., 2010; Ruhl, 2004). However, intra-annual variation related to seasonality or tidal cycles can influence the response of benthic communities (Ruhl, 2004; Tyler, 1988). Canyons can intensify the seasonal upwelling of cold, nutrient rich waters to the surface (Allen et al., 2001; Hickey, 1997), and thus, increase primary production during spring and summer (Granata et al., 2004; Harris and Whiteway, 2011; Macdonald et al., 1987; Ryan et al., 2005). Through both advection and mixing processes, canyons also enhance the exchange of this nutritive material between the shelf edge and the deep ocean (Allen and Durrieu de

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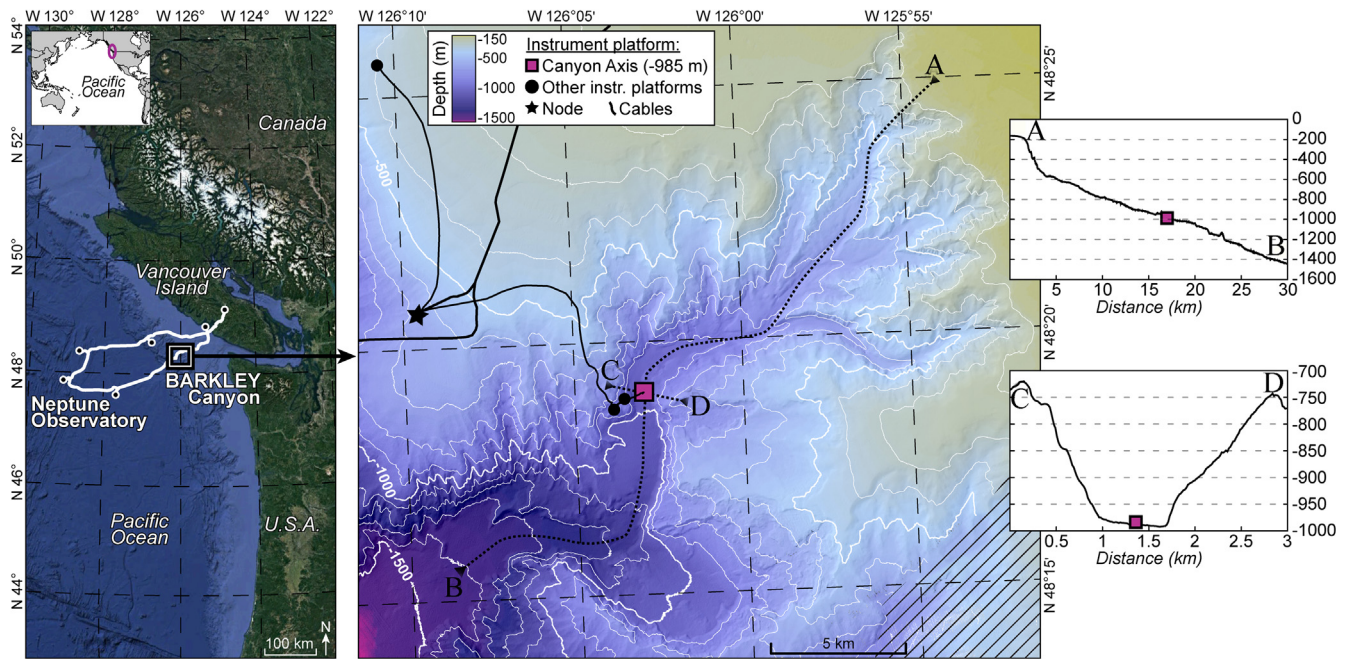


Fig. 1. Location map. Left panel: position of the observatory network Ocean Networks Canada offshore Vancouver Island (BC, Canada). Right panel: bathymetric map of Barkley Canyon showing ONC platforms; the axis (POD1 platform) sampling site, at 985 m depth, is shown as the pink square. Inset side: topography of transects crossing the canyon in length (A-B) and width (C-D). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Madron, 2009), and thus seasonally increase the quantity and quality of nutrient supply in canyons (Gooday, 2002; Vetter and Dayton, 1999; Vetter, 1994). In addition, canyons can act as conduits for particle flux, funneling sediment, nutrient and organic matter (OM) from the continental shelf to the abyssal plain (Nittrover and Wright, 1994; Puig et al., 2014). On the shorter time scales (hours to days) of tidal regimes, internal waves and currents can affect the benthos on the continental margin by modulating daily species activity. For example, patterns such as the nocturnal behavior of the Norway lobster *Nephrops norvegicus* (Aguzzi, 2011; Sbragaglia et al., 2015) or diel displacements of the sablefish *Anoplopoma fimbria* within the canyon axis (Doya et al., 2014) have been observed. More stochastic processes such as benthic storms, river discharge, arrival of big carcasses or even trawling events can also affect deep-sea communities (Almeida et al., 2017; Goffredi et al., 2004; Okey, 1997).

Temporal changes in species distribution also can occur as a consequence of transitions through life history stages. For example, spawning females of the monkfish *Lophius piscatorius* and the hake *Merluccius merluccius* preferentially inhabit canyons compared to the adjacent slope (Farrugio, 2012). Red crabs *Chaceon* spp. show patterns of migration linked to reproduction that, in turn, affect the size structure of the population with aggregating behavior in areas near canyons (López Abellán et al., 2002).

High resolution temporal studies over several years can provide insight into intra- and interannual variation in physical and biological processes affecting ecosystem dynamics. The influence of environmental variability and life histories on community dynamics in canyons is not well known. Short-term studies have suggested a potential impact of the environment on some species on time scales from days to seasons, but those studies covered only few months and were not repeated over multiple years (Juniper et al., 2013; Matasos et al., 2014). Understanding natural variability in canyons is paramount for the prediction of the response of benthic communities to short and long-term change in environmental conditions, and for the assessment of resilience of species and ecosystems.

A large number of canyons incise the continental margin along the west coast of North America (Harris et al., 2014), yet, in terms of fauna,

only few - e.g. Monterey Canyon, California (Lundsten et al., 2010; McClain and Barry, 2010; Ryan et al., 2005) - have been investigated. Since 2009, the Ocean Networks Canada (ONC) observatory has provided continuous interdisciplinary data at various locations west of Vancouver Island (British Columbia, Canada), encompassing coastal areas to the abyssal plain. One of ONC's research themes focuses on the study of benthic-pelagic coupling in Barkley Canyon, a mid-slope submarine canyon for which little ecological data had previously been available (De Leo et al., 2017; Domke et al., 2017). Two major currents drive regional hydrodynamics: the California current which flows towards the equator in summer and the Alaska current flowing in the reverse direction in winter (Freeland et al., 1984). During summer, the upwelling-favorable wind stress, combined with the canyon's topography, directly affects the water column from a depth of 260 m to the sea surface (Connolly and Hickey, 2014). The canyon is considered hypoxic (< 1.40 ml/L) (Grantham et al., 2004), and the entire area is located in the Northeast Pacific Oxygen Minimum Zone (OMZ defined as concentration of Dissolved Oxygen-DO < 0.5 ml/L) (Levin, 2003). Areas within the canyon at similar depths as the ONC platform are mostly inhabited by sea urchins, deep-sea holothurians, pandalid shrimps, gastropods and actinarians (Domke et al., 2017). Improved knowledge of the benthic communities living in the axis of Barkley Canyon and their response to natural variability can help predict how these communities could adapt to changes in regional ocean circulation and the reduction in oxygen recorded in the region (Bograd et al., 2008; Chan et al., 2008). In the hypoxic environment of this submarine canyon, we hypothesized that: (i) the epibenthic megafaunal community would be mainly composed of decapods, gastropods and ophiurids, characteristic of hypoxic zones, as well as of species with adaptations to low oxygen conditions (Domke et al., 2017; Levin, 2003); and (ii) the community might respond to a seasonal signal related to winter/summer variations in nutrient input and changes in hydrographic conditions. Using the ONC platform, and over a period of three years, we: (i) described the community inhabiting the canyon, (ii) characterized the scales of variation in bottom and surface environmental conditions and chlorophyll concentration, and (iii) determined whether environmental forcing drives community dynamics.

Table 1

List of instruments measuring hydrographic parameters at POD1 station (48°19'N, 126°03'W, 985 m depth) from 17 June 2012 to 6 January 2015 at the axis of Barkley Canyon (British Columbia, Canada) and collecting atmospheric information at La Perouse buoy (48°50'N, 126°00'W, Tofino, British Columbia, Canada). We also used 8-day averaged data provided by the MODIS model which uses NASA satellites to obtain surface chlorophyll in a square surface around Barkley Canyon (45°56' to 50°05'N, 124°87' to 132°07'W). BBLc = Benthic Boundary Layer current.

Sampling Site	Instruments Sampling dates	Measured parameters	Sampling frequency	Units
Sea-floor Data	ADCP June-12 to Jan-15	Northward BBLc (Ubar)	10 s	m/s
		Eastward BBLc (Vbar)	10 s	m/s
		Temperature	10 s	°C
	CTD Sept-13 to Jan-15	Pressure	1 min	dbar
		Salinity	1 min	psu
		Conductivity	1 min	S/m
		Density	1 min	kg/m ³
		Temperature	1 min	°C
	Oxygen optode Sept-13 to Jan-15	Oxygen	1 min	mL/L
Weather data	La Perouse Bank buoy June-12 to Jan-15	Significant wave height	1 h	m
		Max. zero crossing wave height	1 h	m
		Wave spectrum peak period	1 h	s
		Direction from which the wind is blowing	1 h	° TRUE
		Horizontal wind speed	1 h	m/s
		Atmospheric pressure	1 h	mbar
Sea-surface Data	NASA Satellites June-12 to Jan-15	Surface chlorophyll concentration	8 days	mg/m ³

2. Materials and methods

2.1. Sampling site

Barkley Canyon is ~42 km long, has a maximum width of 8 km at its head, and incises the continental margin 80 km west of Vancouver Island (British Columbia, Canada) from its shallower rim at ~400 m to the fan at ~2200 m depth (Fig. 1).

The sampling site was located at the canyon axis (latitude: 48°19.0087'N, longitude: 126°03.077'W, depth: 985 m) at the ONC-designated POD1 site. POD1 is a cabled platform equipped with biological and physico-chemical sensors. For more details on the cabled network specifications, see Juniper et al., (2013).

2.2. Data collection

2.2.1. Environmental characterization

The data analyzed in this study were collected from 17 June 2012 to 6 January 2015. The instruments attached to POD1, listed in Table 1, measured: temperature (°C), salinity (psu) and pressure (dbar) at a sampling rate of 1/min; oxygen concentration (mL/L) at 1/min; and

Benthic Boundary Layer currents (BBLc) using a 2-MHz Nortek Acoustic Doppler Current Profiler (ADCP) with temporal and spatial resolutions of 10 s and 1.43 cm, respectively. Atmospheric pressure (dbar), wave height (m) and period (s), and wind speed (m/s) and direction were acquired by NBDC meteorological buoy 46206 on La Perouse Bank (Tofino, British Columbia, latitude: 48°50'24"N, longitude: 126°00'00"W, <http://www.ndbc.noaa.gov>) (Table 1). Surface concentration of chlorophyll was provided as 8-day averages by MODIS, NASA Earth Observations (NEO) Goddard Ocean Color Group (<http://neo.sci.gsfc.nasa.gov>) (Table 1).

2.2.2. Faunal characterization

Five-minute video sequences were recorded every two hours with a color camera mounted on a motorized pan/tilt head allowing for a 360° sweep (all videos are available at <http://dmas.uvic.ca/SeaTube>). Illumination was available on demand from two Deep-Sea Power and Light variable intensity projectors. Because the pan and tilt limit settings for the camera were modified during annual maintenance cruises, the surface area covered by the camera varied between 3.9 m² and 9 m² over the study period (see details in Table 2). For our study, we analyzed the 4th sequence of the day (recorded from 0800 to 0805), every day from 17 June 2012 to 6 January 2015. This time was chosen to minimize the number of gaps in the time series.

Each video was viewed using VLC media player®. All visible fauna (size > 0.5 cm) were counted and identified to the lowest taxonomic rank possible. Because of the challenge to identify individuals at the species level from imagery, we used Operational Taxonomic Units (OTU) when species identification was not possible. We did not collect video information when sediment suspension obscured the seafloor. Density data were obtained by dividing abundance by the surface area of the field of view.

2.3. Data analysis

2.3.1. Environmental characterization

Because the temporal range of the ADCP data acquisition matched the biological sampling period, we used temperature data from the ADCP rather than the CTD (Table 1). Temperature, oxygen, salinity and density were averaged daily. The 10-s ADCP velocity data were first averaged in 10-min intervals, and the resulting values averaged over the full vertical extent of the profile – ~0.2–1.75 m height above bottom – to yield a single time series for each Cartesian component of near-bed velocity. Daily-averaged velocities were then computed from these data and used as up-canyon and cross-canyon Benthic Boundary Layer currents (BBLc). Surface chlorophyll concentrations as provided by NASA Earth Observation (<https://neo.sci.gsfc.nasa.gov>) were already pooled across 8 days with a precision of 0.25°. For these data, we defined a surface area of 144 km² around Barkley Canyon (Appendix A) over which we averaged the data at weekly intervals. Wind speed and direction were pooled using vector averaging to obtain daily-averaged wind speed and direction information. Atmospheric pressure and wave height were also daily averaged. The daily Anomaly of Sea Surface Temperature (ASST) was calculated as the difference between the daily

Table 2

Characteristics of cameras installed at each maintenance cruise (1st- June 2012, 2nd-May 2013 and 3rd-May 2014) at POD1 station at 985 m depth at the axis of Barkley Canyon (British Columbia, Canada). Dates indicate periods in between changes of the camera field of view (for maintenance or technical issues).

Cruises	Dates	Camera	Coordinates	Sweep angle	Surface covered
2012	17 June 12 to 11 May 13	AXIS P1347 SubAqua Im.Syst.Inc.	48.31676 –126.05020	360°	6.1 m ²
2013	12 May 13 to 15 Feb 14	Dragonfish	48.31658	360°	9 m ²
	16 Feb 14 to 05 May 14	SubC Imaging	–126.0502	360°	7.2 m ²
2014	11 May 14 to 11 Aug 14	Dragonfish	48.316644	180° *2	6.1 m ²
	12 Aug 14 to 6 Jan 15	SubC Imaging	–126.050166	100° + 45°	3.9 m ²

mean of Sea Surface Temperature (SST) over the entire time span recorded by the buoy (from 1988 to 2015) and the daily mean of the SST of each date of interest (each day from 17 June 2012 to 6 of January 2015).

For data gaps of less than 5 days, missing values were substituted using k-nearest neighbor modelling (package VIM). The Whittaker-Robinson periodogram (Whittaker and Robinson, 1923) method was used to identify the dominant periods in the environmental variables. The underlying statistic measuring the amplitude used in this periodogram function is the standard deviation of the means of the columns of the Buys-Ballot table (Legendre and Legendre, 2012). The WR periodogram can handle missing values in the datasets. Prior to periodogram analyses, datasets were tested for stationarity. For non-stationary cases, trends were removed by linear regression and residuals were used in the periodogram analysis. Some degree of caution is needed during interpretation as this kind of periodogram also finds the harmonics of basic periods to be significant.

2.3.2. Community dynamics: composition and diversity

We defined major and rare species based on density (abundance per m^2) and species recurrence over time. Species representing less than 5% of the community over the entire period were defined as rare. Conversely, major species represented more than 90% of the community over the entire period. We used Whittaker-Robinson periodograms to identify significant periodicities in changes of density over time for each major species.

Because not all species respond similarly to changes in environmental conditions, particularly depending on their motility, we aggregated the monthly (sum) density of each OTU by motility category to explore a possible temporal trend. Swimmers aggregated all the species able to move against current in the water mass, mostly fish. Walkers represented the species able to walk on the sediment and either jump or swim for short distance, here the arthropods. The species not able to swim against strong current and often observed through the camera as passively moving in the water mass were considered as planktonic. Crawlers grouped all the species able to crawl on the sediment and unable to either jump or swim for even a short distance, mostly gastropods and echinoderms. Correlations between monthly aggregated densities of all categories were tested using Kendall correlations because data were not normally distributed. We used Whittaker-Robinson periodograms to identify significant periodicities in changes of density over time for each category.

To assess temporal patterns in community composition and explore a potential impact of maintenance cruises on these patterns, a multivariate regression tree (Borcard et al., 2011; De'Ath, 2002) was applied to Hellinger-transformed densities (see method description in Appendix B and C). Because none of the identified splits corresponded to the dates of the maintenance cruises, we disregarded a potential observation bias related to maintenance activities or changes in camera position and analyzed the entire time series.

For all multivariate analyses, data were Hellinger-transformed to reduce the importance of double-zeros (i.e., to avoid inferring similarity between sites from double absences) in the data matrix (Legendre and Gallagher, 2001). This transformation preserves the Hellinger distance, which is appropriate in methods based on the Euclidean distance as those used below.

Species diversity was calculated for each day and month, i.e. monthly density is the sum of the 30/31 daily densities. Alpha biodiversity was computed on non-transformed densities using Shannon's and Simpson's diversity indices.

Principal Component Analysis was conducted to visualize the distribution of weekly community composition on the first two principal axes and define potential groups in community composition for each season. To avoid bias due to zero-inflated data and lighten the data matrix, the rare species were removed from the PCA. The aggregation per week was done by summing all daily densities over one week, and

the obtained weekly values were then Hellinger-transformed.

2.3.3. Relationships between community dynamics and the environment

To identify temporal structure in community composition, and the role of potentially important environmental factors regulating this structure, a distance-based Moran's eigenvector maps (dbMEM) analysis was performed. dbMEM, belonging to spatial eigenfunction analyses, computes eigenvectors of spatial configuration matrices and uses them as predictors in linear models (Griffith and Peres-Neto, 2006). Extension to multivariate time series analysis is straightforward (Legendre and Gauthier, 2014) and dbMEM can be used to control for temporal correlation (Peres-Neto and Legendre, 2010). dbMEM is particularly useful for irregularly spaced temporal data (e.g. gaps in sampling dates because of maintenance cruises) (Borcard and Legendre, 2002). The steps involved in the generation of positive dbMEMs (+dbMEMs) (Rádková et al., 2014) are given in Appendix D. Scalograms were used to group +dbMEMs into 3 sub-models (Broad, Medium and Fine), defined as groups separated by non-significant +dbMEMs (Legendre and Gauthier, 2014). The first eigenvectors describe broad temporal structures, i.e., those that encompass several months to a year, while the last eigenvectors describe fine temporal structures (i.e. a few days). To identify the corresponding time periods in each submodel, we computed a contingency periodogram (Borcard et al., 2004). These sub-models were then used as explanatory variables in redundancy analysis to: (1) estimate the percentage of variation in community composition explained by each sub-model; and (2) highlight the relative contribution of each environmental variable to the temporal structure associated with the scale of each sub-model. Partition of the variation in the faunal matrix among the two types of explanatory factor (the environment and the temporal structure), using redundancy analysis ordination (Legendre and Legendre, 1998) was illustrated through a Venn diagram (library *vegan*) (Legendre and Gauthier, 2014). The environmental variables available for the entire time series were the cross-slope and along-slope winds, wave height and period, atmospheric pressure, *in situ* seafloor temperature and the up- and cross-canyon BBLc.

Chlorophyll concentration at the sea surface was tested separately from the other environmental parameters as we only had the weekly averaged values instead of higher daily sampling rates. The response of the four major species to the chlorophyll concentration was tested using Cross Correlation Function (CCF) analysis which gives the correlation between two time series computed as a function of the lag of one with respect to the other (Venables and Ripley, 2002). Because we are interested in the potential influence of chlorophyll concentrations on the density of fauna, only the negative lag will be presented.

3. Results

3.1. Environmental characterization

We used data on atmospheric and *in situ* factors to characterize the environment at our sampling site (Table 3). The weather in the canyon area was characterized by mean wave heights of 2.03 m and wind speeds of ~5.58 m/s (Table 3). The highest wave heights (> 4 m) were recorded in winter (end of November – early December 2012 – February 2013; end of September 2013 – January 2014; December 2014; Fig. 2). In summer, the along-shelf wind speeds were stronger than the cross-shelf winds, and mostly negative, corresponding to upwelling conditions. The reverse was observed in winter (Fig. 2). Periodogram analyses confirmed an annual cycle with significant periods between 276 and 373 days for cross-slope wind, 272 and 382 days for along-slope wind, 271 and 350 days for atmospheric pressure and 262 and 348 days for wave height and period. They also showed significant periods of 289–412 days for sea surface temperature and 312–385 days for the anomaly of sea surface temperature (Appendix D, Fig. D2).

The concentration of surface chlorophyll also followed a seasonal

Table 3

Environmental parameters from 17 June 2012 to 6 January 2015 measured (i) at 985 m depth at the axis of Barkley canyon and (ii) at the sea surface around Barkley Canyon (British Columbia, Canada). Wave height (WH), wind speed (WS), atmospheric pressure (AtmP), sea surface temperature (SST), daily anomaly of sea surface temperature (ASST) parameters are given or derived from hourly data recorded by LaPerouse buoy (Tofino, British Columbia). Chlorophyll (chl) data values are a spatial averaged of a square surface around Barkley Canyon (45°56' to 50°05'N, 124°87' to 132°07'W) obtained from the 8-day averages given by the MODIS model (neo.sci.gsfc.nasa.gov). *In situ* absolute value of BBLc, transverse component (Ubar) and up-canyon component (Vbar) and temperature (Temp) (from June 2012 to January 2015), and oxygen ([O₂]), salinity (Sal) and density (De) (from September 2013 to January 2015) were measured at POD1 ONC observatory site using ADCP for BBLc and temperature, an Oxygen optode and a CTD for the salinity and density. Sd = Standard deviation.

	Surface data						In-situ benthic boundary layer data					
	WH m	WS m/s	AtmP mbar	SST °C	ASST °C	Chl mg/L	[O] mL/L	Sal psu	De kg/m ³	Temp °C	Vbar m/s	Ubar m/s
Min	0.4	0	976.7	7.2	−4	0.29	0.24	34.00	1031	3.51	0	0
Max	8.2	19.1	1045.3	16.7	3.8	7.09	0.34	34.40	1032	4.07	0.2	0.13
Mean	2.0	5.6	1017.6	11.7	−0.2	1.17	0.29	34.38	1032	3.76	0.03	0.02
Sd	1.22	3.57	8.10	2.47	1.60	0.871	0.020	0.023	0.026	0.090	0.020	0.015

pattern with a first peak in April and a second in July every year (Fig. 2); the periodogram revealed an annual cycle with significant period between 51 and 56 weeks (~357–392 days). A maximum concentration of 7.09 mg/L (Table 3) occurred in July 2014 (Fig. 2). The daily anomaly in sea surface temperature started to increase in June 2014 and stayed higher than previous observations until January 2015.

The very low standard deviation of the physico-chemical parameters (temperature, salinity and density) (Table 3) revealed a relative homogeneous BBL environment over the study period (scale of ordinates, Fig. 3). Conversely, BBL currents (BBLc) showed high standard

deviation, however transverse-canyon and up-canyon mean strength were weak and rarely exceeded means of 0.02 m/s and 0.03 m/s, respectively (Table 3, Fig. 3). Over the entire sampling time, the dominant current was oriented down-canyon. The variability in BBL current speed relative to this down-canyon drift was mainly tidal, with amplitudes of 30–70 cm/s (results not shown). On longer time scales – i.e., weeks to months – the magnitude of the velocity variability was < 5 cm/s (Fig. 3). Variations on seasonal and semi-annual time scales, based on 5-days averaged values, had amplitudes of order 1 cm/s (not shown). Oxygen concentration remained below the threshold for

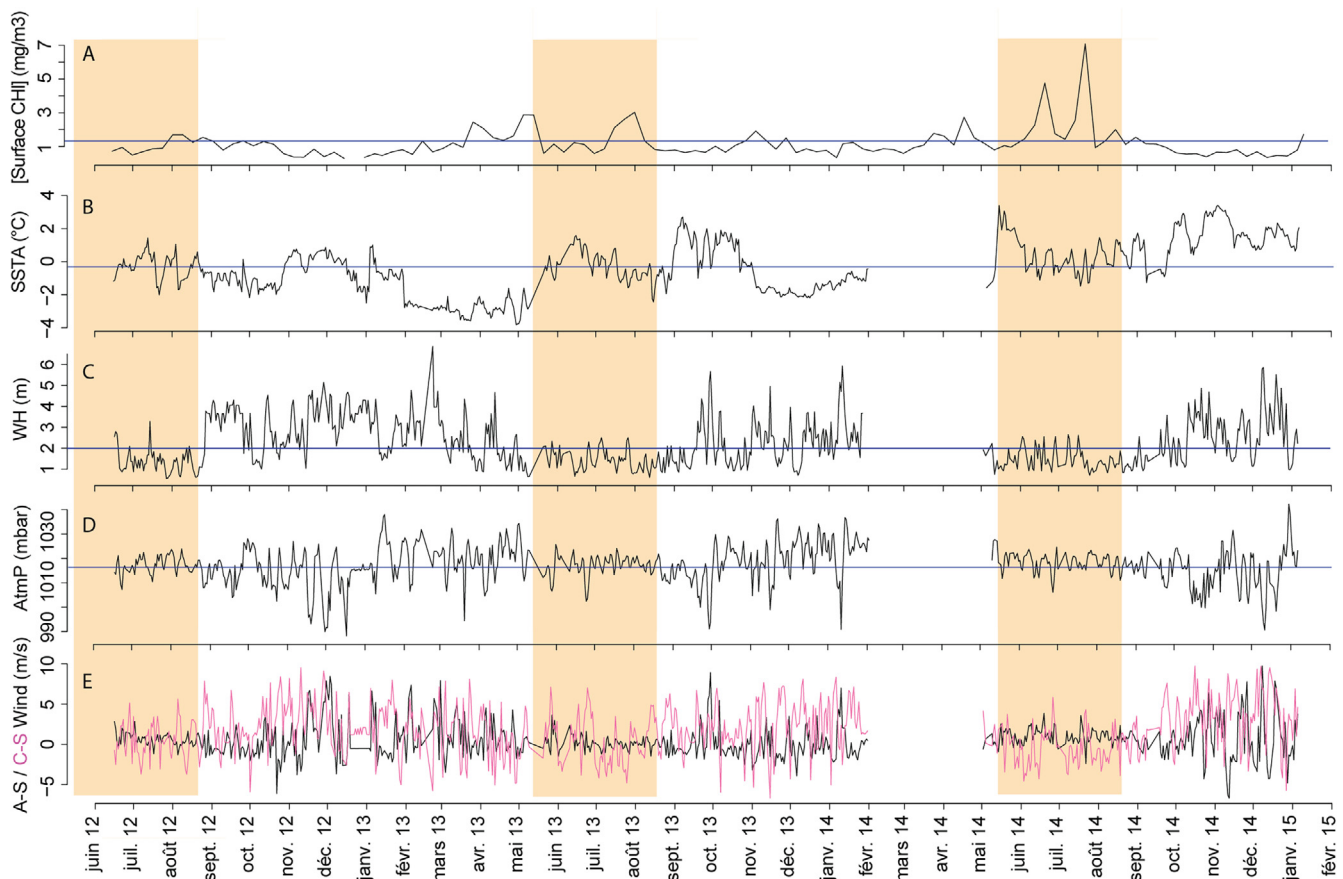


Fig. 2. Time series of A- surface chlorophyll concentration (8-day averaged of a single value representing a sampling in a square surface around Barkley Canyon (45°56' to 50°05'N, 124°87' to 132°07'W) obtained with the MODIS model using NASA satellites, B- Daily anomaly of sea surface temperature obtained from sea surface temperature recorded from 1988 to 2015 by La Perouse buoy (Tofino, British Columbia, Canada), C- wave height (daily averaged) and D- atmospheric pressure (daily averaged) measured by LaPerouse buoy (Tofino, British Columbia, Canada), E- along-slope (black line) and cross-slope (red line) wind (daily vectored averaged). Yellow shading highlights summer time. Blue lines represent the 3 years averages. Sampling dates are from 17 June 2012 to 6 January 2015. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

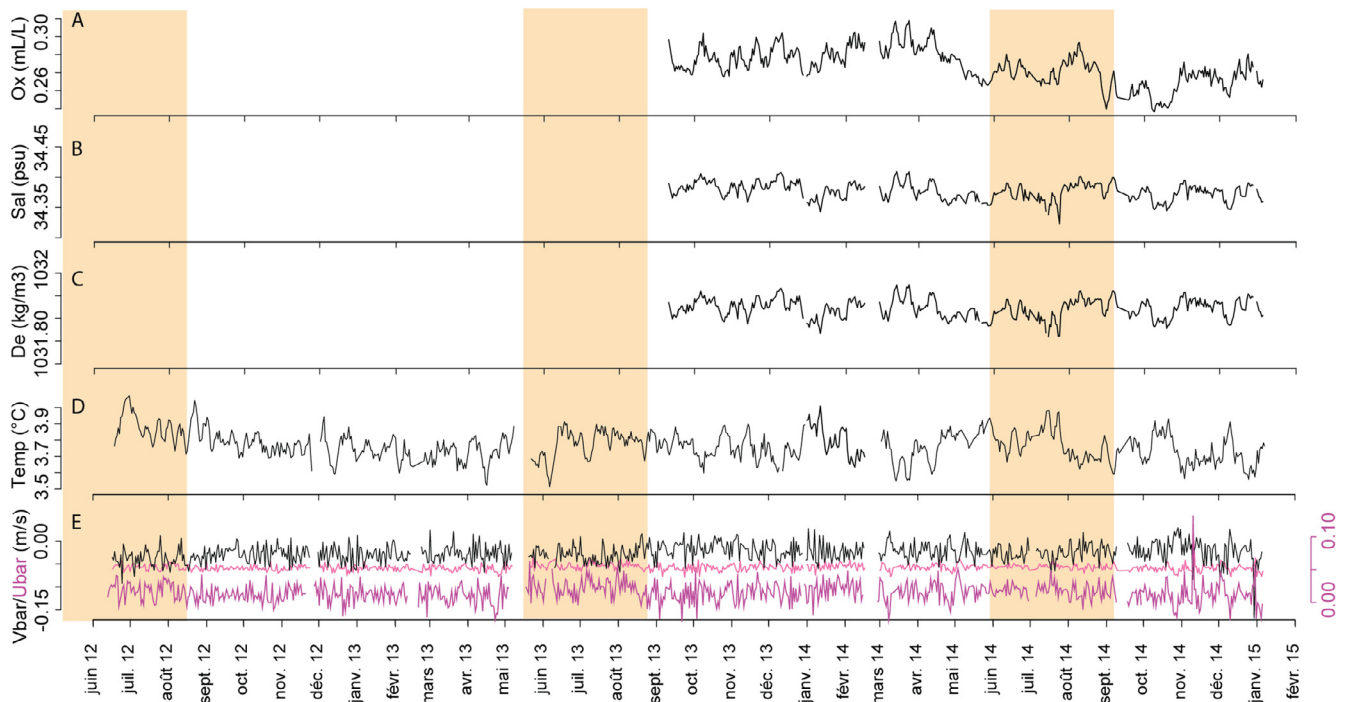


Fig. 3. Time series of in-situ measurements made at POD1 ONC observatory site at the axis of Barkley Canyon (British Columbia, Canada) at 985 m depth using an optode (oxygen), a CTD (salinity and density) and an ADCP (BBLc and temperature). A- Oxygen concentration (mL/L), B- Salinity (psu) C- Density (kg/m³), D- Temperature (°C), E- Up-canyon (black) and transverse- canyon Benthic Boundary Layer currents (m/s). Yellow shading highlights summer time. Sampling dates are from 17 June 2012 to 6 January 2015. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

hypoxia (max = 0.34 mL/L - Grantham et al., 2004) and showed a decrease from April 2014 to November 2014 (Fig. 3). Periodograms performed on BBLc showed three types of significant cycles: a fine scale of 4 days, a medium scale from 159 to 175 days, and a broad scale from 292 to 340 days. Even though amplitude of variation was weak, the physico-chemical parameters (salinity, pressure, density, temperature and oxygen) also showed a broad cycle of 290–400 days.

3.2. Community structure composition and diversity

A total of 72,367 individuals were identified over the 847 days of sampling. We found 28 OTUs, including 4 identified to genus, and 7 identified to species (Table 4). Major and rare species constituted 14% and 46% of the total community, respectively.

Major species included the grooved tanner crab *Chionoecetes tanneri* (> 49,200 observations), the sablefish *Anoplopoma fimbria* (> 10,700 observations), a zooplanktonic species, probably mysids of the genus *Eucopia* (> 4100 obs.), and a species of buccinid or ranellid snails (> 3200 observations in total) (Table 4 and Fig. 4). Periodograms revealed two significant cycles for *C. tanneri*: (i) between 198 and 220, and (ii) 334 and 338 days; and two for *Buccinidae_OTU_2*: (i) 111 and 112 days (and its probable harmonic at 223 days), and (ii) 335 days. No significant cycle was observed for *A. fimbria*. For the Mysids, periodograms revealed finer scale cycles of 7 days (and probable harmonics of 21, 42 and 84 days) (Appendix D, Fig. D5).

C. tanneri and *A. fimbria* displayed the highest densities (Fig. 5). The density of *C. tanneri* showed different peaks during the sampling period with a regular increase in October each year, and highest densities observed in autumn 2014. Density of mysids was very low (< 2 individual/m²) from June 2012 to May 2013, and then steadily increased until the end of the study period. *Buccinidae_OTU_2* had the lowest abundance from June to late July of each year, with this low-density period extending into winter 2013. *A. fimbria* showed no clear intra- or inter-annual pattern in density, although, as for *C. tanneri*, we observed highest density in autumn 2014 (Fig. 5).

When megafauna were grouped by their motility capacity, walkers dominated during the entire sampling period (Fig. 6). The monthly aggregated density of the planktonic category was significantly correlated to that of both walkers and swimmers (Table 5).

Periodograms performed on the monthly aggregated density of each motility group showed no significant periods for walkers and an annual cycle with significant periods of 12, 15 and 11 months for swimmers, crawlers and the planktonic group, respectively (Appendix D, Fig. D4).

Average alpha diversity was 0.5 (min = 0, max = 0.87; 1-Simpson's index) and 1.2 (min = 0, max = 2.4; Shannon's index), with a significant period between 184 and 193 days and an annual period between 312 and 339 days, respectively.

The first two axes of the PCA (Fig. 7) explained 61.5% of the total variance. The first axis separated *C. tanneri* from *A. fimbria* and winter from other seasons. The second axis was associated with decapod shrimps (Hippolytidae) and mysids and separated summer from fall/winter. The overlap between dates of the two principal axes from the different groups can be explained by the temporal continuum between seasons.

3.3. Environmental influence on community dynamics

Cross correlation analysis showed that weekly values of surface concentration of chlorophyll measured in the region of Barkley Canyon were significantly and positively correlated with the density of *Buccinidae_OTU_2* (CCF = 0.2) with a lag of 2 months, and with a lag of 5 months with the densities of *C. tanneri*, mysids and *A. fimbria* (CCF = 0.35, 0.30 and 0.49 respectively).

A total of 196 positive and 651 negative dbMEMs were found. Redundancy analysis (RDA) selected the 78 significantly positive dbMEMs that were used to model the faunal matrix. Most of the temporal structure in the variation of community composition was broad scaled (i.e., captured by significant dbMEMs with the lowest values), and the remainder was divided between medium and fine scales (Fig. 8). Periodograms revealed two cycles with periods of

Table 4

List of benthic megafauna recorded at the axis of Barkley Canyon (British Columbia, Canada) at 985 m depth from 17 June 2012 to 6 January 2015 and identified to the lowest taxonomic rank possible. Species considered as major are highlighted in blue and those considered as rare in grey. Buccinidae_OTU_2 could also be a member of the Ranellidae family. Actinarians were always observed on Buccinidae_OTU_2 shell and are thus categorized as crawlers.

Phylum	OTUs name	Total of observations	Motility
Chordata	<i>Anoplopoma fimbria</i>	10740	Swimmer
	<i>Sebastolobus</i> sp.	11	Swimmer
	<i>Coryphaenoides</i> sp.	125	Swimmer
	<i>Bothrocara molle</i>	24	Swimmer
	Eelpout_OTU_1	781	Planktonic
	<i>Lycodapus</i> sp.	2	Swimmer
	<i>Lycenchelis</i> sp.	27	Swimmer
	<i>Eptatretus</i> sp.	99	Swimmer
	<i>Careproctus melanurus</i>	1	Swimmer
	<i>Bathylagonus nigripis</i>	32	Swimmer
Mollusca	Buccinidae_OTU_1	1124	Crawler
	Buccinidae_OTU_2 or Ranellidae_OTU_1	3217	Crawler
Arthropoda	Paguroidea	98	Walker
	<i>Chionoecetes tanneri</i>	49298	Walker
	Galatheididae	283	Walker
	Hippolytidae	1070	Walker
	Caridae	782	Walker
	Mysids: ? <i>Eucopia</i> spp.	4172	Planktonic
	Pandalidae	2	Walker
Echinodermata	Asteroidea_OTU_1	38	Crawler
	Solasteridae	2	Crawler
	Ophiuroidea	2	Crawler
Cnidaria	Actinaria	82	Crawler*
	Scyphozoa	197	Planktonic
	<i>Poralia rufescens</i>	130	Planktonic
Ctenophora	Ctenophora	23	Planktonic
Annelida	Polychaete	3	Crawler/Swimmer

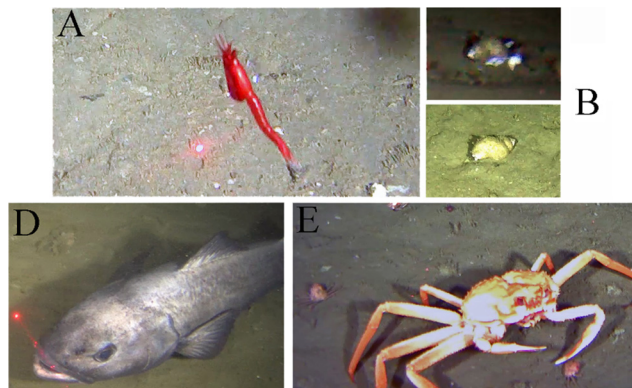


Fig. 4. Images of the major species observed with a stationary video camera at the axis of Barkley Canyon (British Columbia, Canada) at 985 m depth from 17 June 2012 to 6 of January 2015. A Mysids, likely *Eucopia* spp; B Buccinidae_OTU_2; D *Anoplopoma fimbria* and; E *Chionoecetes tanneri*.

212–243 days and 342–346 days for the broad scale sub-model, 46–51 days for the medium scale and 8 days for the fine scale (Table 6).

The variation partitioning of the megafaunal time series with respect to environmental (i.e. up and cross canyon bottom boundary layer (BBL) current, temperature, wave period, wave height, and wind speed, anomaly of sea surface temperature and sea surface temperature) and MEM model explanatory variables (based on significant positive dbMEMs only) revealed that 61% of the variation remained unexplained. Only 0.4% of variation was explained by the exclusive effect

of the environmental variables and 8% by the combined effects of environmental parameters and temporal structure. Thirty percent of variation was explained by the temporal model only. The broad sub-model accounted for most of the variation in the community (27%), whereas the medium and fine scale sub-models accounted for only 3 and 4%, respectively. Shared effects of environmental factors and the broad-scale sub-model explained 8% of the variance (all tested factors were significant) (Table 6). The combination of wave height, anomaly of sea surface temperature and *in situ* bottom temperature significantly explained 0.5% of the medium-scale temporal sub-model and none of the fine-scale sub-model (Table 6). This shift in the benthic community temporal structure and environmental conditions is consistent with the cycle lengths revealed by the periodograms for all environmental factors (between 290 and 400 days). For all species (except Buccinidae_OTU_2), species' density was significantly positively correlated with the ASST (Table 7).

4. Discussion

This study is based on long term multidisciplinary data (3 years), sampled at high frequency (daily) at 1000 m depth in a canyon on a continental margin, and as such addresses repeated recommendations to better understand natural variability of deep-sea ecosystems in an integrated way (Levin et al., 2016; Levin and Le Bris, 2015; Lochte and Pfannkuche, 2002; Markus et al., 2017). The high resolution enabled detection of temporal cycles and structure over a wide range of scales from days to years in environmental and biological data. While previous studies have highlighted the role of tidal-related cycles on animal communities in different deep-sea environments (Cuvelier et al., 2014; Doya et al., 2014; Lelièvre et al., 2017; Wagner et al., 2007), including at Barkley Canyon (Doya et al., 2014; Matabos et al., 2014), most were too short to resolve longer period variations, such as seasons, or to validate observations on longer time scales such as inter-annually. However, several factors inherent to the use of fixed deep-sea camera systems limited our ability to generalize our results: the spatially restricted and varying area of sampling (< 10 m²), the size of organisms large enough to be visible on video (here > 0.5 cm), and the inability to identify species to low taxonomic levels. The structure of the instrument array itself could have influenced organismal behavior and consequently community composition. The use of lights for the camera could disrupt normal behaviors of certain species, such as avoidance of white lights by *Anoplopoma fimbria* (Widder et al., 2005), or have no influence on others such as for *Chionoecetes* crabs (Watanabe, 2002). Although Vardaro et al. (2007) showed the absence of a structural effect on abyssal fish and echinoids at 4100 m depth, to our knowledge, no study has been published on taxa known to aggregate, such as crabs (Stevens et al., 1994; Stone et al., 1993) and buccinids (Martell et al., 2002). In any case, any effects related to the presence of the platform are expected to be consistent over time, and changes observed over the 3 years of study to be biologically relevant (Matabos et al., 2012).

4.1. Environmental characterization

Weather and sea surface parameters (atmospheric pressure, along- and cross-canyon wind, wave height and period and sea surface temperature) showed significant temporal cycles of ~1 year (300–400 days), likely as a result of seasonal variation in surface conditions in the region (Allen et al., 2001; Connolly and Hickey, 2014; Foreman et al., 2011). This intra-annual variation is related to climatic forcing, causing changes in wind and surface currents between summer and winter. The upwelling-favorable wind conditions observed in summer during our study are characteristic of the Northeast Pacific coast and consistent with previous studies conducted in the region (Allen et al., 2001; Hickey, 1997; McFarlane et al., 1997; Tinis et al., 2006). The upwelled, cold, nutrient rich water (Hickey and Banas, 2008; MacIsaac et al., 1985) supports the phytoplankton blooms

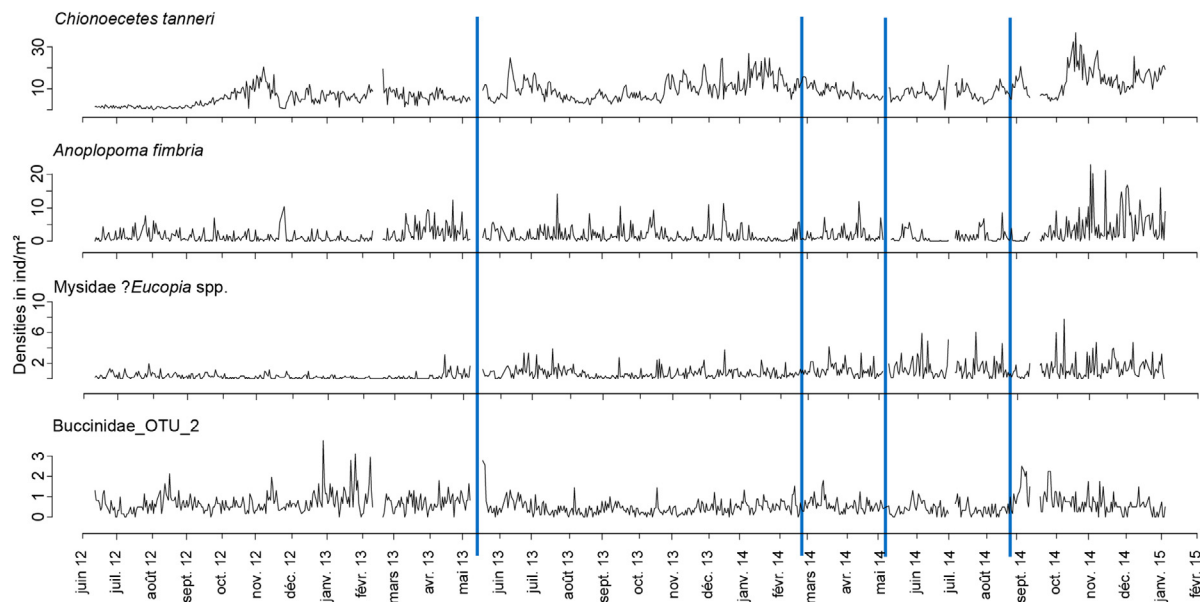


Fig. 5. Time series of density (ind/m²) of major species recorded with a stationary video camera at the axis of Barkley Canyon (British Columbia, Canada) at 985 m depth from June 2012 to January 2015. The mysids were probably? *Eucopia* spp. Blue vertical lines indicate a change in camera parameters which modified the field of view and/or the area coverage. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

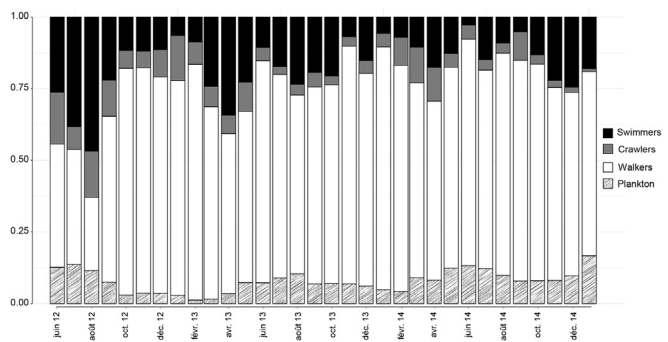


Fig. 6. Cumulative frequency of species density aggregated by their motility type and by month, sampled once per day with stationary video camera from 08 h 00 to 08 h 05 (UTC) at 985 m depth at the axis of Barkley Canyon from 17 June 2012 to 6 January 2015.

Table 5

Results of the correlations performed on the densities of all OTUs aggregated by month and motility at 985 m depth at the axis of Barkley Canyon (British Columbia, Canada) from 17 June 2012 to 11 January 2015. T = Kendall rank correlation coefficient and «ns» = non-significant.

	Swimmers		Planktonic		Crawlers	
	T	p-value	T	p-value	T	p-value
Walkers		ns	0.46	0.000	0.24	0.050
Swimmers			0.31	0.012		ns
Planktonic						ns

measured between April and June of each year. During winter, downwelling-favorable conditions (northward, along shelf-break wind) (McFarlane et al., 1997; Tinis et al., 2006), combined with storm events, tend to enhance mixing processes within the upper layer of the water column (Dagg, 1977), in turn increasing downward particle flux (Zùñiga et al., 2009) in canyons. In Barkley Canyon, this phenomenon was reported by Thomsen et al., (2017) and also observed in this study. Starting in December, this process can impact the phytoplankton biomass, and the export of primary production on short temporal scales as

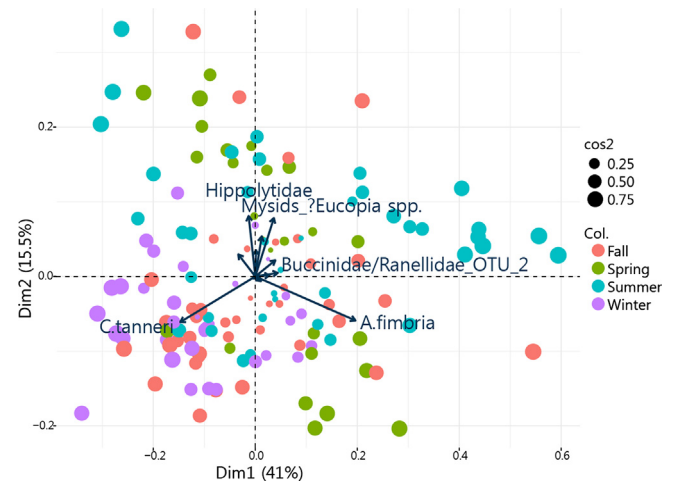


Fig. 7. PCA performed on megafaunal density recorded with a stationary video camera from 08 h 00 to 08 h 05 (UTC) every day from 17 June 2012 to 6 January 2015 at 985 m depth at the axis of Barkley Canyon (British Columbia, Canada). Daily values were aggregated by week (sum) then transformed according to Hellinger. The arrows represent species that contributed to the observed variance. Species near the origin of the axes were removed to improve clarity. The size of the points is a function of cos2, indicating the quality of its representation on the chosen dimensions.

short phytoplankton pulses followed by low pressure systems are expected to reach our sampling site as pulses of fresh organic matter in 12 to 72 h (Thomsen et al., 2017).

The axis of the canyon at 985 m depth is located below the upwelling depth at 250 m (Allen et al., 2001) and within the core of the Oxygen Minimum Zone (in OMZ [O₂] < 0.5 ml/l (Domke et al., 2017; Levin, 2003). The very low oxygen measured over the three years is similar to the one measured a year earlier at the same site (Juniper et al., 2013), supporting a strong inter-annual stability of the OMZ within the canyon. Annual cycles were also significant in the Bottom Boundary Layer (BBL) suggesting the occurrence of seasonal variation. Mean near-bed flow was 2–4 cm/s, and down-canyon in all seasons and all three years; the variability in current speed relative to this down-

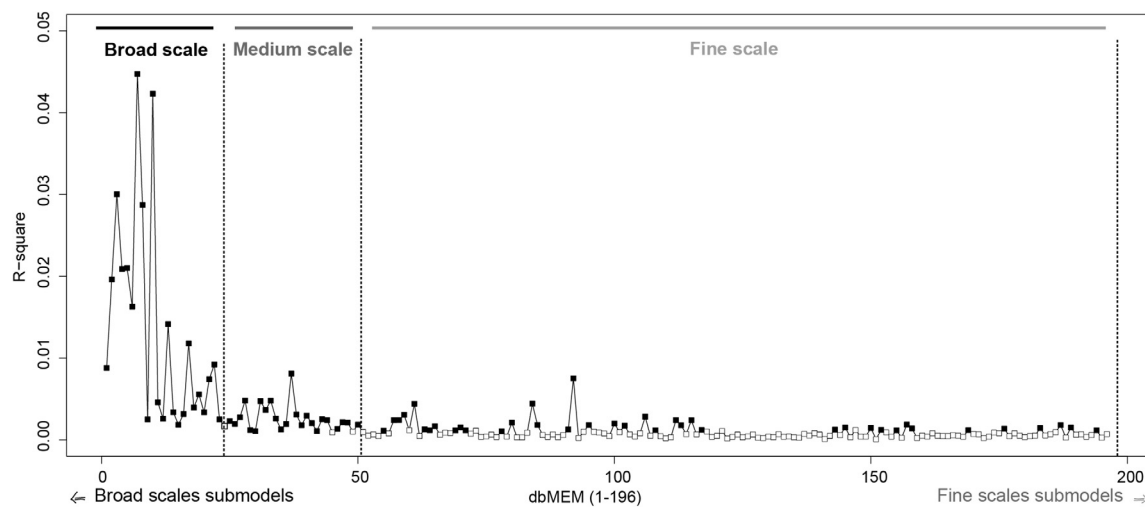


Fig. 8. Scalogram illustrating the scaling of temporally structured variation in benthic megafauna community data at the axis of Barkley Canyon (British Columbia, Canada) sampled with a stationary video camera at 985 m depth every day from 08 h 00 to 08 h 05 (UTC) from 17 June 2012 to 6 January 2015. Values on the ordinate are semi-partial R^2 (i.e., the variation explained by individual dbMEM variables), computed separately for each dbMEM eigenfunction with positive Moran's I (1–196). The statistics of the dbMEM that were selected by forward selection (i.e. the 78 that significantly contributed to model the faunal response data) are represented by black squares.

Table 6

R^2 and probabilities related to the temporal analysis of the epibenthic megafaunal community sampled with a stationary video camera from 08 h 00 to 08 h 05 (UTC) every day at 985 m depth at the axis of Barkley Canyon (British Columbia, Canada). First line: R^2 of each spatial sub-model. Second line: R^2 of the regression of the sub-model (fitted values) on a subset of backward-selected environmental variables. Third line: product of the two previous lines, i.e. variation of the community data explained by the environmental variables at the scale considered. Other lines: p-values of the regression coefficients of the environmental variables in the model considered. (***) for p-value < 0.0001; ** for p-value < 0.05, / for non-tested as R^2 was = 0).

	Axis community	Broad	Medium	Fine
Significant period (days)		212–243 342–346	46–51	8
R^2_{adj} of dbMEM submodel on axis community		0.269	0.0373	0.044
R^2_{adj} of environment on submodel		0.080	0.008	0.0004
R^2_{adj} of environment on axis community	0.004	0.022	0.0003	0.00001
Wave height	***	***	***	/
Wave period	***	***		/
Anomaly of sea surface temperature	***	***	***	/
Sea surface temperature	***	***		/
Atmospheric pressure	***	***		/
Along-slope wind	***	**		/
Cross-slope wind	**	**		/
Up-canyon boundary layer current	**	**		/
Cross-canyon boundary layer current	**	**		/
Temperature	***	**	***	/

canyon drift was mainly tidal. Variations on seasonal and semi-annual time scales are barely discernible and, if present, have amplitudes of order 1 cm/s. The amplitude of seasonal variations in the measured physico-chemical parameters was weak, suggesting that the axis of the canyon is relatively stable in terms of environmental conditions with a local temperature around 5 °C, and a severe hypoxia (0.30 ml/L).

These homogeneous conditions could however be impacted by the variation in surface chlorophyll concentration through heterogeneous arrivals in quantity and quality of OM along time in the BBL of the axis.

4.2. Characteristics of the epibenthic megafaunal community in Barkley Canyon

From the 28 OTUs identified, 4 dominated the epibenthic megafaunal community, i.e. the crab *Chionoecetes tanneri*, the fish *Anoplopoma fimbria*, mysids (probably *Eucopia* spp.), and an OTU belonging to buccinid or rannelid family of gastropod. These results corroborate previous observations in Barkley Canyon (Juniper et al., 2013), and in Monterey Canyon (California, USA) around whale carcasses at 2018 m depth (Lundsten et al., 2010). Also, ROV surveys

confirmed the presence of rannelid gastropods and *C. tanneri* in the core of the OMZ between 800 m and 1000 m depth in the axis of Barkley Canyon (De Leo et al., 2017; Domke et al., 2017). Studies based on IOV survey at the wall of the canyon near cold seeps also confirmed the

Table 7

Results of the correlations performed between daily anomaly of sea surface temperature -calculated using sea surface temperature (°C) measured from 1988 to 2015 at LaPerouse buoy (Tofino, British Columbia, Canada) - and the daily densities of major OTUs observed at 985 m depth in the axis of Barkley Canyon (British Columbia, Canada) from 17 June 2012 to 11 January 2015. T = Kendall rank correlation coefficient and «ns» = non-significant.

	ASST	
	T	p-value
<i>A. fimbria</i>	0.06	0.014
<i>C. tanneri</i>	0.14	1.40e–09
Mysids? <i>Eucopia</i> spp.	0.17	1.60e–12
Buccinidae_OTU_2		ns

presence of buccinid gastropods, *C. tanneri* and *A. fimbria* but in different proportions than in our observations (Doya et al., 2017). The differences in species composition and observational patterns warrants caution when comparing data recorded with fixed cameras to those from moving platforms (towed camera, IOV, ROV, AUV), especially for highly mobile species. For example, large variation in sampled area prevents us from comparing local (alpha) biodiversity with these studies (Ramirez-Llodra et al., 2010; Vetter et al., 2010). In our study, the dominance of hypoxia-tolerant taxonomic groups associated with only a few other taxa, can be explained by low dissolved oxygen concentrations characteristics of OMZ (De Leo et al., 2017). The major taxa found at the axis of the canyon have morphological or physiological adaptations to low oxygen concentrations. For example, adults of the sablefish *A. fimbria* exhibit weight-specific oxygen consumption rates which reduce metabolic rates (Sullivan and Smith Jr., 1982), along with large gill surface areas observed among OMZ populations (Friedman et al., 2012). All individuals of the grooved tanner crab *C. tanneri* were immature in our study - i.e. < 100 mm (Keller et al., 2016; Workman et al., 2002). No studies exist on physiological or morphological adaptations of *C. tanneri* to hypoxia, but the presence of immature individuals only may suggest that those stages are less sensitive to low oxygen. A higher resistance of juveniles has been observed in gastropods (Vosloo et al., 2013), but juveniles of different crustacean species, such as shrimps and blue crabs, avoid hypoxic regions altogether (Stickle et al., 1989). Alternatively, immature crabs may be using the canyon as shelter from predation by large fish that avoid the OMZ as they are more vulnerable and less foraging-efficient in hypoxia (Ekau et al., 2010; Pollock et al., 2007). Mysids can show important ventilation associated with larger gills and efficient respiratory pigment when found in a hypoxic area (Levin, 2002; Sanders and Childress, 1990). Buccinidae and ranellidae can endure low oxygen levels (Theede, 1973) and are commonly found in hypoxic zones, for example *Jerrybuccinum kantori* in the Chilean coast (Fraussen et al., 2014), *Neptuna* spp in Monterey Bay (California) (Braby et al., 2007) and *Fusitriton oregonensis* in Barkley Canyon (De Leo et al., 2017; Domke et al., 2017).

4.3. Scales of variation in the community dynamics

Temporal structure explained 35% of the variance in the epibenthic megafaunal community in Barkley Canyon. Most of this variance (i.e. 27%) corresponded to a broad scale of 225 (+/- 15) and 344 (+/- 4) days, most likely an annual cycle that we hypothesized is related to seasonal variation. This hypothesis is strengthened by the highly significant correlation between the broad temporal scale and all measured surface and benthic boundary layer (BBL) hydrographic conditions. While analyses do not provide information on the mechanisms behind the observed dynamics, results suggest a strong influence of surface primary production. This hypothesis was supported by the strong link between all major species and the surface chlorophyll concentration with a lag of 2–5 months. Despite the lack of quantitative measurements of the input in organic material, peaks in primary production recorded at the surface are expected to impact and reach the BBL in the axis of Barkley Canyon (Campanyà-Llovet et al., 2018; Thomsen et al., 2017). Indeed fresh organic material of phytoplanktonic and zooplanktonic origin was found around 800 m depth in Barkley Canyon and attributed to different sources: (i) sinking of phytoplankton from the surface and re-suspended material from shallower sites and, (ii) overwintering migration of copepods (Campanyà-Llovet et al., 2018). The amount and timing of surface production reaching these depths in the canyon will depend on topography and resuspension events under elevated flow (Thomsen et al., 2017). In our study, only 8% of the broad scale temporal sub-model is explained by the measured environmental conditions. But because of the difference in temporal sampling rates, the

surface production was not included in the analyses. Thus, part of the remaining variance could be attributed to the surface production, but also to other processes such as biotic interactions (e.g. predation, reproduction), occurring on seasonal scales. For instance, the intra-annual variation in crab density might reflect spatial movement of the population in response to resource availability. The seasonal increase in the density of juvenile of *Chionoecetes tanneri* in June and October, likely also observed shallower on the canyon wall (Doya et al., 2017), might be related to the arrival of the spring and summer surface phytoplankton blooms. Immature tanner crabs feed mostly on zooplankton (Phillips and Lauzier, 1997), accounting for the positive correlation with the planktonic group, which also increases during blooms (Burghart et al., 2010; Fulmer and Bollens, 2005; Roe, 1984). In addition, seasonal reproduction matching the timing of the spring bloom could explain the recruitment of young crabs in fall, in an area where they find refuge from predation. The seasonal pattern in faunal distribution we observed supports the hypothesis of seasonality proposed by Juniper et al. (2013) after a year of observations on the wall of Barkley Canyon. Similarly to our observations, those authors also noted that some species showed no temporal patterns but occurred throughout the year. The absence of a seasonal signal in the abundance of the sablefish *A. fimbria* could be related to their high mobility (Sullivan and Smith Jr., 1982). Their opportunistic predatory behavior may explain the absence of an annual temporal pattern in abundance (Friedman et al., 2012; Sullivan and Somero, 1980). Over the three years, the combination of both environmental conditions and temporal components explained 39% of the variation in megafaunal community, suggesting the important role of factors, such as other environmental variables, biotic interactions, life-history traits, and stochastic events and random processes.

In autumn 2014, a sudden increase in the density of *C. tanneri* was concomitant with higher variability in density of *A. fimbria* and *Eucopeia* spp., and a spring/summer peak in surface chlorophyll concentration. The high surface primary production observed in summer 2014, was associated with a greater daily anomaly in sea surface temperature compared to previous years. This phenomenon coincided with the “Blob”, i.e. the strongest temperature anomaly event recorded since the 1980s, which started in winter 2013–2014 in the NE Pacific Ocean, characterized by warm surface temperature (2 °C above average near-surface temperature anomalies), and a shallower mixed layer (5–10 m shallower) (Bond et al., 2015). Those abnormal values were observed until the end of 2014. Our results suggest that species in the canyon indirectly responded to this climatic anomaly through increased resource availability. Alternatively, the suppression of nutrient transport into the mixed layer (Bond et al., 2015) could have affected the diel vertical migration of the mysid prey and in turn altered their behavior and probably that of other zooplankton species. However, the processes and mechanisms underlying this community response remain to be determined. The trend observed in this study underlines the need to monitor future changes in environmental conditions in the region and the associated ecological responses. The combined effect of expanding OMZs (Whitney et al., 2007) and surface temperature warming in response to global change might precipitate the system into an alternative state with strongly modified community structure and ecosystem functions (Scheffer et al., 2001) if the system reaches its tipping point (van Nes et al., 2016).

5. Conclusion

This study revealed that the benthic community at 1000 m depth on the axis of Barkley Canyon is mainly composed of taxa adapted to severe hypoxic conditions and of, at least, two species of commercial interest: *Chionoecetes tanneri* and *Anoplopoma fimbria*. The community

exhibited an annual cycle in density that can be partly attributed to seasonal changes in sea surface weather and hydrographic conditions both at the sea surface and in the benthic boundary layer. Transport of nutrients from the sea surface to the seafloor is suggested to be the main mechanism regulating community dynamics. Despite strong seasonal trends, environmental conditions at 980 m depth on the axis of Barkley Canyon are homogeneous over the year, allowing species to adapt to this hypoxic environment. Lastly, an increase in the sea surface temperature anomaly attributed to the 'BLOB' led to changes in the benthic community composition, probably in response to an increase in surface production and/or a modification in nutrient transport. Our results underscore the need for long-term monitoring in the region, and a better understanding of ecosystem resilience to impacts related to climate change.

Acknowledgments

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Appendix A. Appendix: Map of surface chlorophyll

Fig. A1.

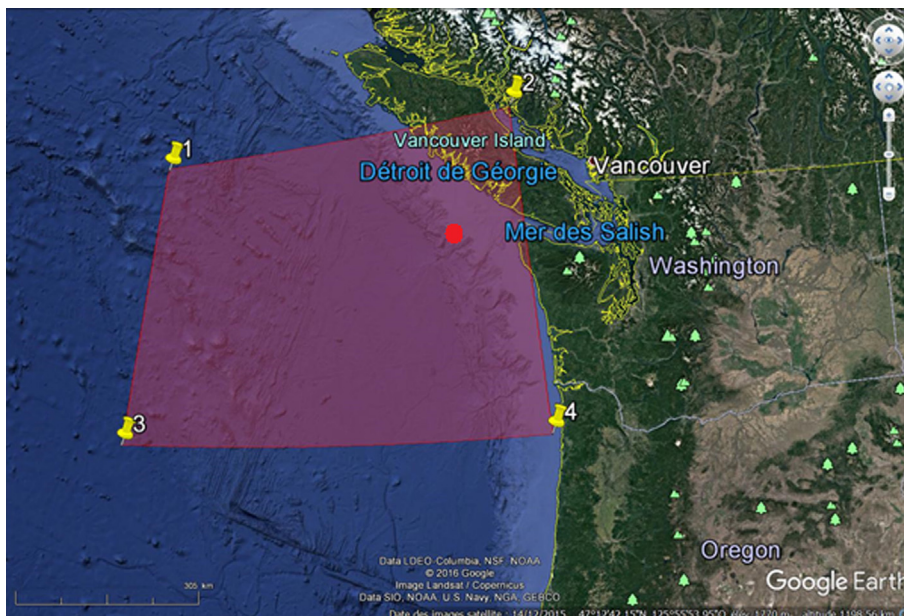


Fig. A1. Map of the surface used to obtain one single value of chlorophyll concentration for the analysis. Chlorophyll (*chl*) data are a spatial averaged of the square surface around Barkley Canyon (red square surface = 144 km²). Coordinates of point 1 = 49°5'21.50"N; 132°4'5.62"E, point 2 = 50°3'9.32"N; 124°52'6.47"E, point 3 = 45°13'34.96"N; 132°36'51.32"E, point 4 = 45°34'6.82"N; 124°7'52.19"E. The chlorophyll concentration is obtained from the 8-day averages given by the MODIS model which uses NASA satellites (neo.sci.gsfc.nasa.gov). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Appendix B. Appendix: MRT analysis

Fig. B1.

The following paragraph is the method describing Multivariate Regression Tree analysis we used to verify a potential impact of the maintenance cruise on the temporal patterns observed in the community composition.

MRT result is a tree whose terminal groups of sites are a subset of sites chosen to minimize the within-cluster sums of squares and where each successive partition is defined by the dates (Borcard et al., 2011). The contribution of each node to the explained variance is called complexity (the sum of those complexity gives the overall R^2). The “discriminant” species at each node are identified by selection of the species contributing the most to the variance down to a minimum of 10.

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Competing interests

No competing interests to declare.

Conflicts of interest

None.

Author's contribution

P.C., M.M. and A.M. conceived the ideas and contributed to the interpretation of the results. P.C. collected and analyzed data. A.H. analyzed and interpreted current and wind data. A.M. and M.M. supervised the research project. All authors assisted in the writing process and revised the manuscript.

MRT on megafauna density data
Explanatory variable = days

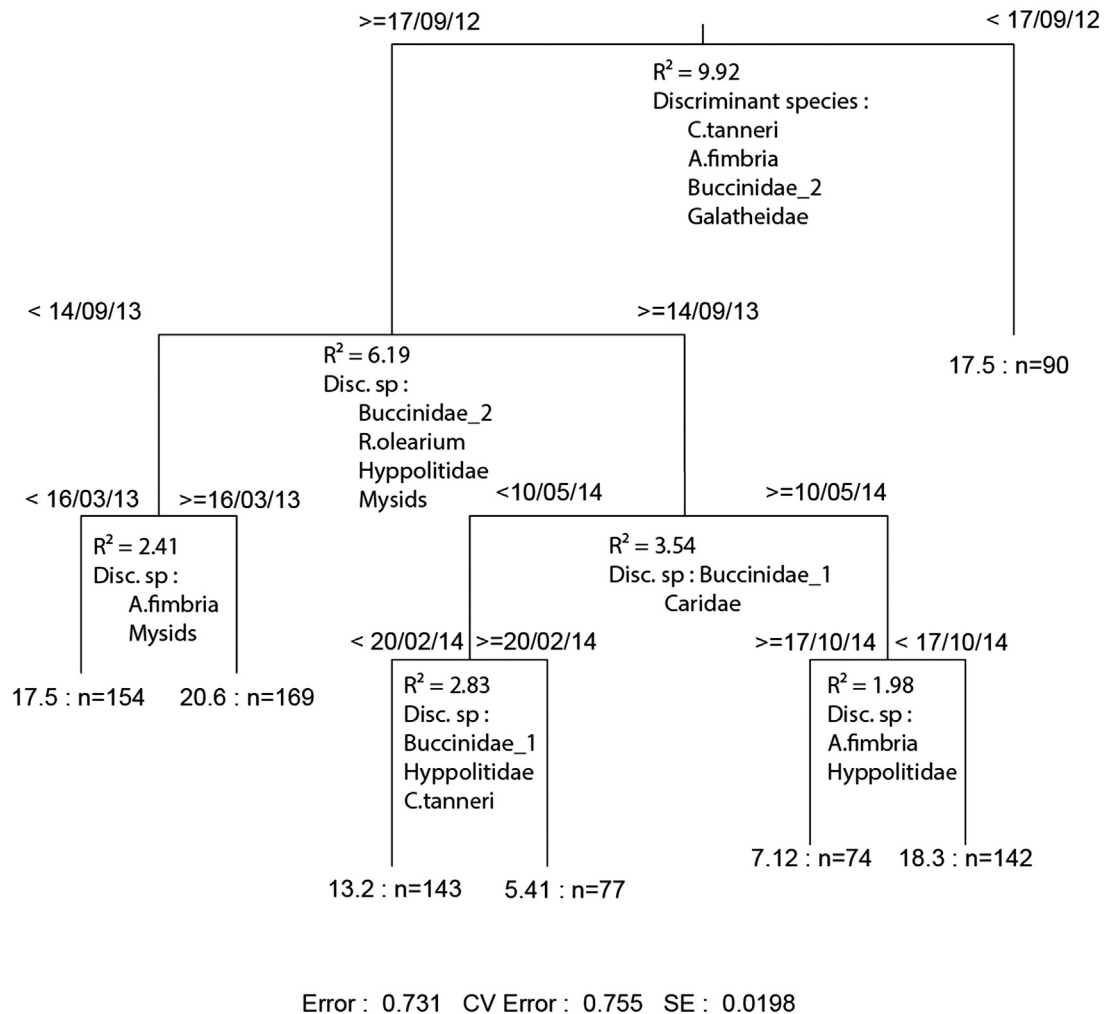


Fig. B1. Results of the MRT analysis performed on megabenthic community sampled from 17 June 2012 to 6 January 2015 in at 985 m depth from 08 h 00 to 08 h 05 with a stationary video camera at the axis of Barkley Canyon (British Columbia, Canada). For each node the R^2 (contribution of each node to the explained variance) and discriminant species are shown.

Appendix C. Appendix: DbMEM method

The following paragraph is the method describing DbMEM analysis used to identify temporal structure in the community composition and the role of environmental factors driving these patterns:

The steps involved in the generation of dbMEM are (Rádková et al., 2014):

1. Starting from the dates of the sampling period (1 sample per day from June 2012 to January 2015: $n = 847$), a Hellinger distance matrix D was calculated for all possible distances d_{ij} between sampling dates i and j .
2. A temporal connectivity function W was constructed by truncating D at a distance dt (Borcard and Legendre, 2002; Dray et al., 2006; Griffith and Peres-Neto, 2006), which is either equal to or larger than the length of the longest link in the minimum spanning tree on D (this length represents the shortest distance required to maintain the network of all dates connected) (Borcard et al., 2004). In essence, W is a truncated matrix in which only some dates are connected. Each non-null weight w_{ij} indicates the possible connection between dates i and j , and the actual value of w_{ij} illustrates the strength of the potential interaction between the two temporal units i and j (Dray et al., 2006).
3. A principal coordinate analyses applied to the truncated Euclidean distance matrix W generated the eigenvectors (dbMEMs). The procedure yields both positive and negative eigenvalues. DbMEMs paired with positive eigenvalues depict a positive temporal association, whereas dbMEMs paired with negative eigenvalues depict a negative temporal association (Griffith and Peres-Neto, 2006).

4. Significance of the dbMEMs was tested with a forward selection. The significant positive and negative dbMEMs were used as explanatory variables in Redundancy analysis (RDA) to estimate the percentage of variations in community composition explained by temporal structure.

For our analyses, we only focused on positive temporal association (i.e., +dbMEM). A scalogram of the relative importance of the +dbMEM eigenfunctions was plotted. The contributions of the eigenfunctions to modelling the variation of the community series are given by the semipartial R^2 of each MEM, but the significance is the one found during forward selection of the eigenfunctions.

Appendix D. Appendix: Periodogram figures

Figs. D1–D5.

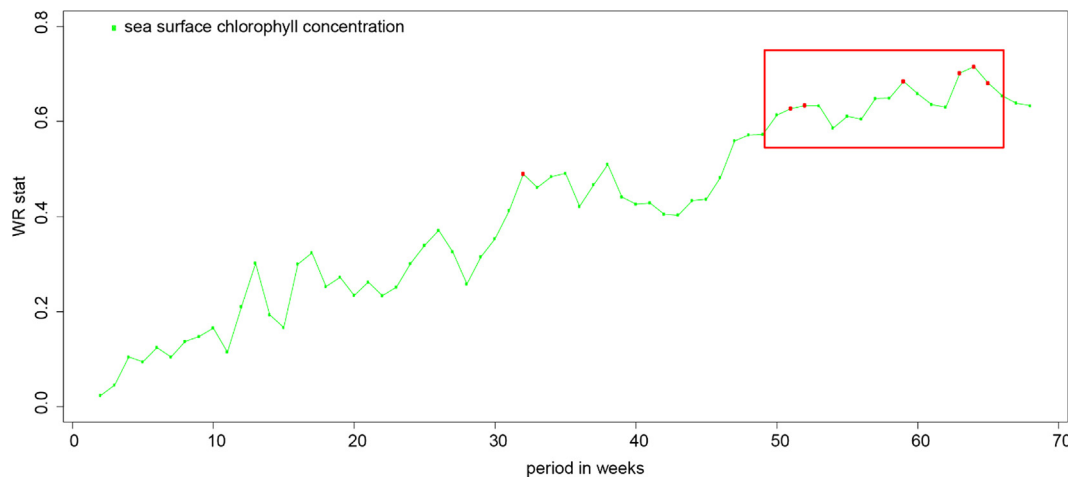


Fig. D1. Whittaker-Robinson periodogram statistics computed for sea surface concentration in chlorophyll, featuring periods comprised between 2 and 68 weeks. Red squares indicate periods that are significant at the 5% level. Chlorophyll (chl) data values are a spatial averaged of a square surface around Barkley Canyon (British Columbia, Canada; 45°56' to 50°05'N, 124°87' to 132°07'W) obtained from the 8-day averages given by the MODIS model (neo.sci.gsfc.nasa.gov). The red box delineates a high density of significant periodicities corresponding to the annual cycle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

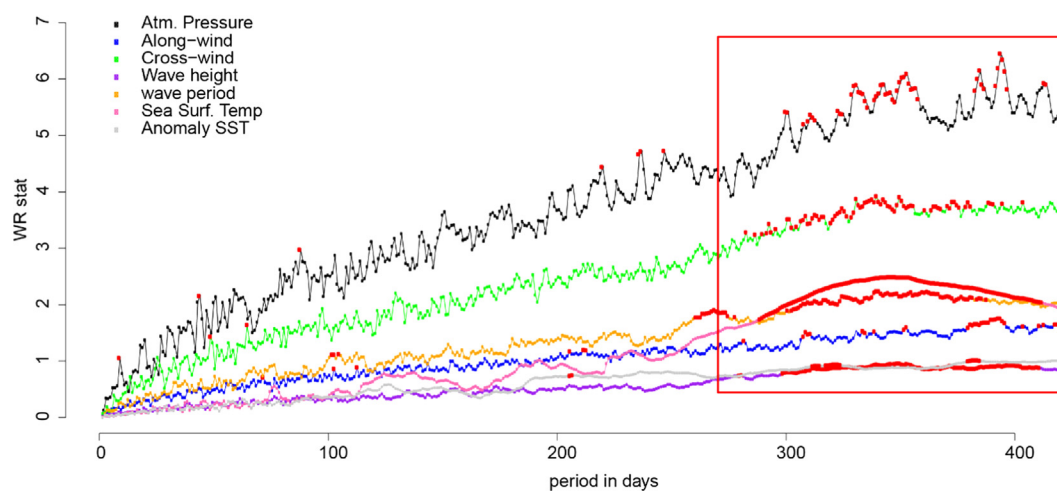


Fig. D2. Whittaker-Robinson periodogram statistics computed for sea surface and weather parameters, featuring periods comprised between 2 and 423 days. Red squares indicate periods that are significant at the 5% level. Wave height, wind speed, atmospheric pressure, sea surface temperature, anomaly of sea surface temperature (Anomaly SST) parameters are given or derived from hourly data recorded by LaPerouse buoy (Tofino, British Columbia, Canada). The red box delineates a high density of significant periodicities corresponding to the annual cycle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

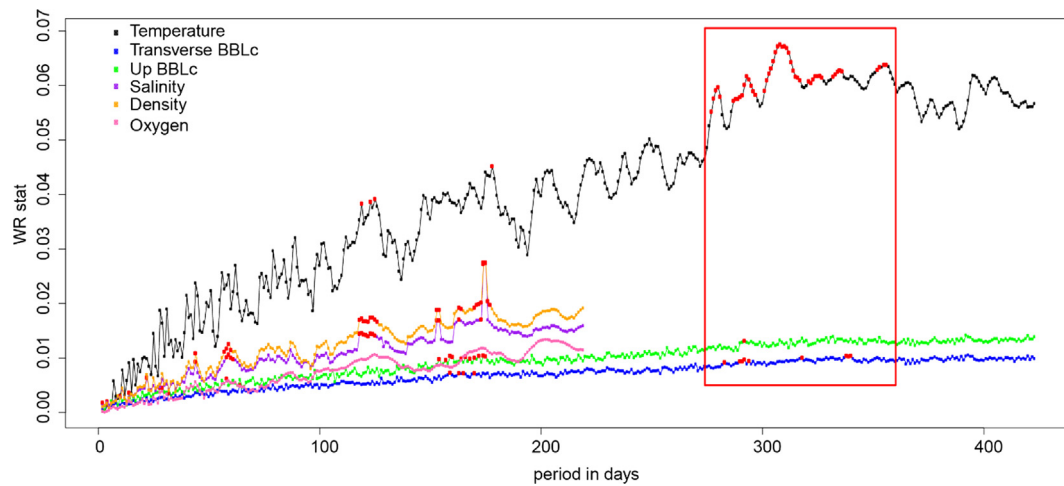


Fig. D3. Robinson periodogram statistics computed for *in situ* bottom parameter, featuring periods comprised between 2 and 423 days for Temperature and Benthic Boundary Layer currents (BBLc) and between 2 and 219 days for Salinity, Density and Oxygen. Red squares indicate periods that are significant at the 5% level. *In situ* BBLc, transverse component and up-canyon component and temperature (from June 2012 to January 2015), and oxygen, salinity and density (from September 2013 to January 2015) were measured at POD1 Ocean Networks Canada observatory site (British Columbia, Canada) using an ADCP for BBLc and temperature, and an oxygen optode and a CTD for the salinity and density. The red box delineates a high density of significant periodicities corresponding to the annual cycle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

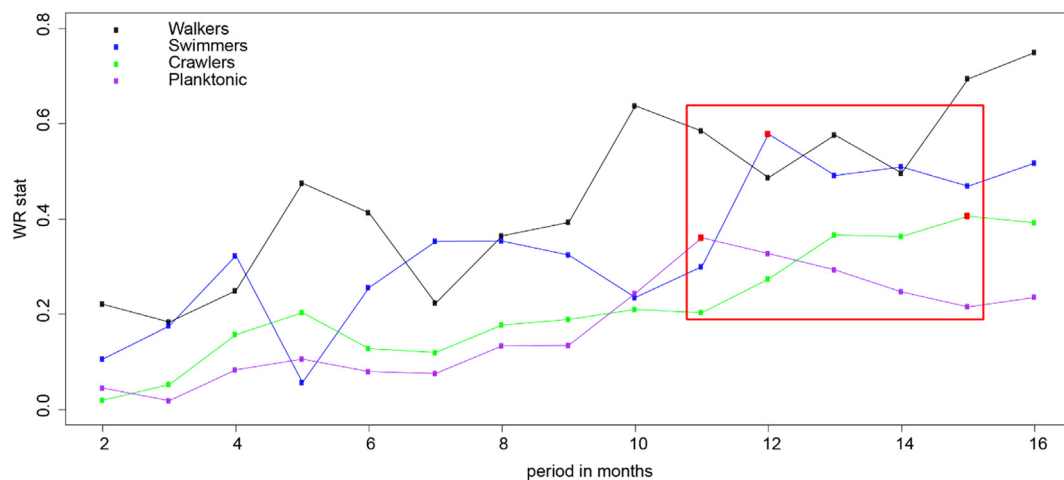


Fig. D4. Whittaker-Robinson periodogram statistics computed for motility categories featuring periods comprised between 2 and 16 months. Species density were aggregated by their motility type and by month, sampled once per day with stationary video camera from 08 h 00 to 08 h 05 (UTC) at 985 m depth at the axis of Barkley Canyon (British Columbia, Canada) from 17 June 2012 to 6 January 2015. Red squares indicate periods that are significant at the 5% level. The red box delineates a high density of significant periodicities corresponding to the annual cycle. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

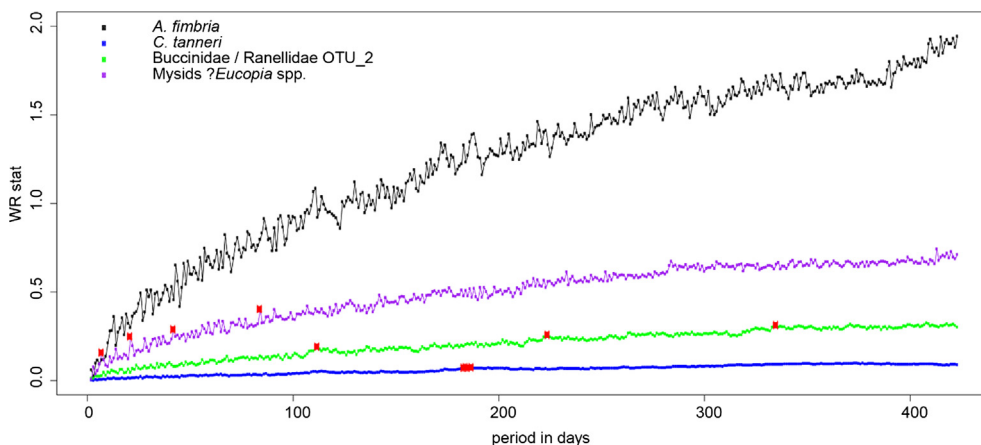


Fig. D5. Whittaker-Robinson periodogram statistics computed for major species densities, featuring periods comprised between 2 and 423 days. Red squares indicate periods that are significant at the 5% level. Densities were obtained from fauna sampled once per day with stationary video camera from 08 h 00 to 08 h 05 (UTC) at 985 m depth at the axis of Barkley Canyon (British Columbia, Canada) from 17 June 2012 to 11 January 2015.

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